FACTORS INFLUENCING FUNGUS SUCCESSION ON DUNG CULTURES

By WILLIAM H. BROWN and PAUL W. GRAFF

(From the Botanical Section of the Biological Laboratory, Bureau of Science, Manila, P. I.)

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FACTORS INFLUENCING FUNGUS SUCCESSION ON DUNG CULTURES

By WILLIAM H. BROWN AND PAUL W. GRAFF

(From the Botanical Section of the Biological Laboratory, Bureau of Science, Manila, P. I.)

The phenomenon of succession, or the gradual replacement of one association of plants by another, is of widespread occurrence and probably effects the distribution of almost all kinds of plants. Owing, perhaps, to the greater prominence of the vascular plants, the phenomenon has been studied chiefly in connection with these; but it is by no means confined to them. It is a well-known fact that a number of fungi occur in a rather definite succession on horse dung when placed in a moist chamber. The first to appear usually belong to genera of the *Mucoraceae*. These die down and are followed by a variety of forms which vary with the conditions. In Manila this stage is usually represented by the genera *Oospora*, *Botrytis*, *Sordaria*, and others in less quantity. After this several species of *Coprinus* usually appear and may continue to produce fruit bodies for a considerable period. The succession is frequently much more complicated than that outlined above.

Successions of flowering plants are frequently due to geologic factors such as the weathering or erosion of the soil. In other cases, the primary causes of a succession consist of changes in purely physical factors produced by its first members. Examples are the increasing of the water-holding capacity of soils by the accumulation of vegetable matter and the binding of wind-blown sand. It would seem evident that neither of the above classes of factors could be operative in the case of the succession here considered.

There are, however, a number of theories which are frequently advanced in explanation of the succession of vascular plants; and which, on theoretical grounds, might be considered as possibly applicable to successions such as the one described above. Some of the most prominent of these may be mentioned. The death of the first plants of a succession is frequently caused by the competition of those representing a later stage. In this case the

success of the latter plants may be due to the fact that the first have altered the soil in such a manner that it will support them. Many writers have advocated the view that when one plant grows on a soil for a considerable length of time it removes certain nutritive substances to such an extent that it is no longer able to make a vigorous growth. Others have held that plants excrete substances which are toxic to the species which excretes them, but may not produce harmful effects in other plants. These last two hypotheses have naturally frequently been used to explain the same phenomena. Another factor which might affect successions of either vascular plants or fungi is the growth of microörganisms in the soil. In the case of the succession under consideration it is also necessary to consider the possible effect of the drying out of the substratum. The object of the present paper is to decide which, if any, of the above hypotheses will furnish a solution of the cause of the succession of fungi on dung cultures.

The work here reported was carried on at the Bureau of Science, Manila from January to June, 1912.

EXPERIMENTATION

On the 29th of January a collection of horse dung was made from the streets of Manila. Twenty cakes were placed in the sun and left until their outer surfaces became slightly dry, after which they were distributed, five in each of four covered glass dishes. By the next day there were signs of two mucors which later proved to be *Mucor racemosa* Fres., and *Absidia caerulea* Bain. On the second day there was a fair growth of both molds and slight signs of *Oospora* sp. By the third day the two mucors had made their maximum growth which, however, was not very vigorous. The *Oospora* continued to increase in abundance for several days longer. On the fourth of February, at the end of six days, *Coprinus stercorarius* Fr. and *C. plicatilis* Fr. appeared in the cultures. By this time the growth of the mucors had decreased markedly and they died out three days later. The *Oospora* disappeared a few days after the molds, while the fruit bodies of the two species of *Coprinus* continued to be produced for two months, which was as long as the cultures were kept. During the latter part of this period other fungi appeared in the cultures but in minor quantities.

Twelve other cultures were run with dung obtained from the stable of the Bureau of Science. The results in all cases were essentially similar to those just described. In some of the dishes only one of the mucors appeared, while in one, the two were

accompanied by a species of *Pilobolus*. In a few cases species of *Botrytis* and *Sordaria* appeared along with *Oospora*, while other species of *Coprinus* sometimes took the place of those previously mentioned. The succession described in detail thus appears to be characteristic of what may be expected to occur in Manila and was therefore made the basis of further work.

Pure cultures of each of the five fungi were kept growing on agar, the fungi being transferred to fresh tubes as often as was necessary to keep them in good condition. All inoculations made in the experiments were from these pure cultures. The dung used was obtained from the stable of the Bureau of Science and so should have been substantially similar in all cases.

Since the mucors were the first of the fungi both to appear and disappear the experiments were directed largely toward discovering the cause of their early death. The first question considered was the possibility of this having been due to toxins which the plants themselves might have excreted. In order to test this six cakes of dung were placed in each of four covered glass dishes. The dishes and dung were then sterilized to kill all organisms contained in them. This was accomplished by heating in an autoclave for fifteen minutes at 120° under a pressure of one kilo. On the 7th of February two dishes were inoculated with *Mucor racemosa* and two with *Absidia caerulea*. On the third day after inoculation the growth of the mucor was in every case much greater in all dishes than that which had occurred in any of the unsterilized cultures and continued to be healthy for eight weeks. After this the substratum dried out and they gradually ceased growing but appeared to be alive at the end of another month. Twelve other sterile cultures were run at various times in Erlenmeyer flasks the bottoms of which were covered with a layer of dung 2 cm deep. These gave results very similar to those just described. It is to be noted that the mucors on the sterile dung were still alive even after the substratum had apparently become air dried while those on unsterilized dung always disappeared completely in less than ten days. This, together with the much more vigorous appearance of the former, would seem to show that the death of the molds in the original cultures could hardly have been due to toxins which they excreted. It would also appear that these facts exclude the idea that the mucors could have used all of the food material which was suitable for them.

The results in the original cultures could moreover not have been due to differences in the amount of water in the substratum.

It was noted that fresh dung which had not been allowed to dry out to some extent, before being placed in covered dishes, never produced any mucors even when inoculated with the spores or hyphae. Moreover, when unsterilized dung, even after being slightly dried, was mashed, mixed, and placed in an Erlenmeyer flask the growth of molds which appeared on it was always very scanty. This also appeared to be due to an excess of moisture, for a slight drying does not greatly affect more than the superficial layers and the mixing of the mashed dung causes a redistribution of the moisture. It would appear, however, that the presence of the moisture is in itself not the cause of the detrimental effects observed, for a vigorous growth of molds was always produced on sterilized dung, and while it was found that sterilizing in an autoclave produced only slight changes in the amount of moisture it did increase it. The probability is that the excessive amount of moisture favored the growth of other organisms which were detrimental to the growth of the mucors. This point will be discussed later. It is to be noted further that sterilized dung, even when fairly dry, produced a luxuriant growth of mucors and that they persisted on it until the dung was apparently thoroughly air dry, while they always disappeared from the unsterilized dung in less than ten days and while it was still quite moist.

The experiments already mentioned having apparently eliminated the possibility of the mucors causing their own death in the original cultures by either excreting toxins or using up all of the available food supply, it became advisable to test the effect of the growth of the other fungi on both of the molds. This was done on dung in Erlenmeyer flasks. This method proved to be particularly convenient as infections could easily be prevented, and so it was used almost exclusively in subsequent experiments. Fresh dung was collected, dried slightly, then mashed and thoroughly mixed, and a layer about 2 cm deep placed in the bottoms of the flasks. The mouths of the flasks were then plugged with absorbent cotton. Two of the flasks were kept as checks and the others sterilized by heating in an autoclave for fifteen minutes at 120° under a pressure of one kilo. This same method was always followed when Erlenmeyer flasks were employed.

In order to test the effect of the growth of the fungi on *Absidia caerulea,* fourteen 600 cc flasks were prepared as above on the thirteenth of March. Two were kept as checks and twelve sterilized. The latter were inoculated in duplicate on March 18th, as follows: 1, *Absidia caerulea;* 2, *A. caerulea* and *Mucor*

racemosa; 3, *A. caerulea* and *Oospora* sp.; 4, *A. caerulea* and *Coprinus stercorarius;* 5, *A. caerulea* and *Coprinus plicatilis;* 6, all five of the fungi mentioned above.

The growth in the unsterilized checks was quite similar to that in the unsterilized cultures previously described. There was a growth of mucors followed by *Oospora* and this in turn by *Coprini.* The growth of the mucors and *Oospora* was very scanty and disappeared in less than ten days.

The mucors and *Coprini,* with which the sterile dung was inoculated, commenced to grow immediately and in three days there was a vigorous growth of both. The growth of *Oospora* was not visible as soon as that of the other fungi, owing probably to its small size. The mucors reached their maximum development in five, and the *Coprini* in ten days. The growth of the individual fungi was in every case much greater than in any unsterilized check, while the total growth on the sterilized was always many times greater than on the unsterilized dung. There were so few hyphae in the unsterilized dung that they might easily have been overlooked on superficial examination, while in the sterilized they were so abundant that a compact felt was produced. In the flasks containing the *Coprini* this was so dense even after drying that water poured on the surface of the felt did not penetrate into the interior. All of the fungi moreover remained alive until after the substratum had apparently become air dry. Since *Absidia caerulea* grew very much better when grown on sterilized dung with any of all of the other fungi than it did in any of the unsterilized checks, and showed no signs of dying except with the drying out of the substratum, it would seem that neither any nor all of these fungi could have produced the deleterious effect observed. The vigorous growth of *Mucor racemosa* with all of the other fungi would indicate that the same thing was true in the case of this species, while the vigorous growth of the *Coprini* would, likewise, seem to show that the sterilization of the substratum was favorable to the vegetative development of these. They, however, produced very few fruit bodies, which would seem to be due to the vigorous growth of the hyphae having exhausted the substratum of food or moisture, before reaching the fruiting stage.

The growth of *Absidia caerulea* on the sterilized substratum appeared to be inversely proportional to that of the other fungi. It grew best when alone; next with *Oospora* which is a small and slow growing fungus; and poorest when with all of the other four fungi. *Mucor racemosa* is a much larger and more rapidly

growing species than *Absidia caerulea* and with it *A. caerulea* made a poorer growth than with any other single fungus. The *Coprini* finally produce a very rank growth, but at first are slow growing, which would seem to account for the fact that with them *Absidia caerulea* made a better growth than with *Mucor racemosa.* Owing to the slight difference in the appearance of the various fungi it is difficult to compare the total amount of hyphae in the flasks but it is doubtful if this varied far from the average in any of them.

These cultures of *Absidia caerulea* alone and with the other fungi show quite clearly that there may be a sharp competition between the various fungi growing in succession on dung, but at the same time they show equally clearly that this competition cannot explain the behavior of this mold on unsterilized dung.

Another series similar to that last described was run in duplicate in 450 cc Erlenmeyer flasks. The results appeared to be in every way similar to those just described except that the fungi were less vigorous in the 450 cc flasks than in those holding 600 cc. This difference in vigor was probably connected with the amounts of food and air available in the two sizes of flasks.

The experiments already reported having apparently proved that the early disappearance of *Absidia caerulea* in unsterilized cultures could not have been due to the presence of the other fungi considered, it remained to be seen if the same thing would hold for *Mucor racemosa.* On the 14th of March fourteen 600 cc flasks, containing dung, were prepared as described in the experiments with *Absidia caerulea,* two being kept as checks and 12 sterilized. The checks showed a succession similar to that described for other unsterilized cultures. This consisted of mucors followed by *Oospora* and this in turn by *Coprini.* The growth of the mucors and *Oospora* was very scanty and disappeared completely in nine days.

The sterilized flasks were inoculated in duplicate as follows: 1, *Mucor racemosa;* 2, *M. racemosa* and *Absidia caerulea;* 3, *M. racemosa* and *Oospora* sp.; 4, *M. racemosa* and *Coprinus stercorarius;* 5, *M. racemosa* and *Coprinus plicatilis;* 6, all of the five just mentioned. The results obtained were quite similar to those given in the case of *Absidia caerulea.*

The mucors and *Coprini* commenced to grow immediately and in three days had made a vigorous growth. As in the cultures of *Absidia,* the growth of *Oospora* did not become visible as soon as the other fungi, probably owing to its small size. The mucors apparently reached their maximum development on the

fifth and the *Coprini* on the tenth day. In every case the fungi made a much greater growth than in the unsterilized flasks, and continued to appear vigorous until after the substratum had become air dry. In this case, as in the previous flasks with *Absidia caerulea*, the growth of the hyphae of the *Coprini* was so vigorous that dense felt-like masses were formed, whereas these hyphae could not be distinguished in a superficial examination of the unsterilized cultures, the presence of the *Coprini* being recognized only by their fruit bodies.

The total growth of hyphae was many times greater in all of the sterilized flasks than in any of the unsterilized ones. As in the case of *Absidia caerulea*, the amount of growth made by *Mucor racemosa* varied inversely to that of the other fungi. The greatest growth of *Mucor racemosa* was obtained when it was grown alone, the next best with the small and slow growing *Oospora*, and the poorest with all of the other fungi. The growth with *Absidia caerulea*, *Coprinus stercorarius* and *C. plicatilis* was about equal and intermediate between that with *Oospora* and with all. It is probable that the total amount of growth did not vary greatly in any of the flasks.

Series similar to the above were run in duplicate in both 450 and 1,000 cc flasks. The results obtained from these appeared to be entirely similar to those just given, except that the individual fungi made a greater growth in the 600 cc than the 450 cc flasks and a still greater growth in those holding 1,000 cc. As in the case of the preceding series, this was probably due to the different amounts of food and air present in the different flasks.

The experiments with *Mucor racemosa* show that when this species is grown with other fungi there is a sharp competition which results in a retardation of its growth but at the same time the results do not explain its behavior in the unsterilized cultures. In the latter it made a very spindling growth and always disappeared in less than ten days while when grown on sterile dung with any or all of the fungi considered the growth was many times as great as on the unsterilized media and, moreover, continued to be vigorous until the substratum had apparently become air dry.

The experiments, so far reported, would seem to show that the succession of the fungi on the unsterilized dung was not due to any of three causes which are probably most frequently offered in explanation of the successions of higher plants, these being; the depletion of nutrient materials by the first plants of the succession; by the plants producing toxins which cause

their own disappearance; by the competition of the later plants of a succession when the substratum is prepared for them. They also show that variations in the moisture content of the substratum are not responsible for the succession.

The order in which the fungi become visible in the unsterilized cultures would appear to be due to their various rates of growth and not to some having started before the others. The mucors on sterilized media grow rapidly and fruit in three days. *Oospora* grows much more slowly and so does not become visible until after the molds. The difference in the rates of growth of these fungi on agar in test tubes is very striking. In three days the mucors fill the tubes while in the same time *Oospora* makes only a slight growth. The hyphae of the *Coprini* grow rapidly from the first on sterilized dung, while they can be distinguished only with difficulty in unsterilized cultures. In either case it takes them about ten days to fruit. It will thus be seen that their presence in unsterilized cultures would not be recognized until they had fruited or, in other words, not for ten days.

The difference in the growths obtained on sterilized and unsterilized dung would seem to show that the disappearance of the mucors and *Oospora* in the latter case was due to microorganisms in the substratum. Probably the chief effect of sterilizing is the killing of all of the organisms. We have seen that the changes in the moisture content of the dung are insignificant, and it is not likely that the food supply is altered sufficiently to explain the results. A great variety of microörganisms occur in the dung in large numbers. These would certainly compete with the fungi for food and oxygen and in all probability would also excrete toxic substances which would be detrimental to them. If these microörganisms are allowed to remain in the dung for ten days it will not support the Mucors even when inoculated with them. If now it is sterilized with either steam, chloroform or formalin, which three methods were tried, it will again support a vigorous growth of fungi. The steam might cause the volatilization of toxic organic compounds but it is not likely that the latter would be destroyed by both chloroform and formalin. From this it would seem that the removal of the competition of the microörganisms is sufficient to prevent the early disappearance of the molds, but it is also quite probable that the microörganisms excrete substances which are harmful to the fungi although definite proof of this is lacking.

From the foregoing it is evident that the order in which the fungi appear in unsterilized cultures is due to their different

rates of growth, and the disappearance of the mucors and *Oospora* to the presence of microörganisms in the substratum. The *Coprini* appear to be more resistant to the effect of the microörganisms although the growth of their vegetative hyphae is greatly disminished.

The deleterious effects which the microörganisms have on the growth of the fungi under consideration is apparently quite similar to their action on vascular plants. The fungi may themselves excrete toxic compounds but the effect of such substances must be small when compared with that of the microörganisms.

SUMMARY

The succession of fungi on dung cultures in Manila is very similar to that reported from temperate regions. Typically it consists of Mucors followed by *Oospora* and in turn by *Coprini*. The Mucors and *Oospora* disappear in less than ten days while the fruit bodies of the *Coprini* are produced over a considerable period.

The order in which the fungi become visible is probably due to their different rates of growth, while the disappearance of the *Mucors* and *Oospora* is connected with the presence of microorganisms in the substratum.

The fungi considered may excrete toxic substances, and in all probability diminish the food supply, but neither of these factors appear to be influential in causing the succession. When the mucors are grown on sterilized dung they make a growth many times greater than on unsterilized and, moreover, continue to appear vigorous until after the substratum is apparently air dry.

The competition of the other fungi considered, causes a restriction in the growth of the mucors on sterilized dung. This restriction is, however, so slight as to apparently exclude the idea that such a competition may be the cause of the death of the molds in the unsterilized cultures.

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